INHERITANCE IN THE "WALKING-STICK," APLOPUS MAYERI.

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The family Phasmatidæ, as is well known, shows some of the most striking cases of "protective resemblance" found among the insects. Several of the genera are typically stick-like to a surprising degree while members of the genus *Phyllium* resemble in detail a leaf-like structure. These animals are no doubt protected by their imitative forms provided they behave in a certain manner. In fact the protection or concealment of such an animal depends as largely on its behavior as upon its resemblance to surrounding objects. In order to ascertain whether these so-called protectively adapted insects really exhibited a "protective behavior" I [1] studied the habits of the "walking-stick," *Aplopus mayeri*, which is abundant on the Tortugas Islands, Florida. These large insects were found to behave in a manner almost ideal for their concealment among the twigs and stems of the plant on which they feed, *Suriana maritima*.

My study was made during a season, June and July, when the enemies of *Aplopus* were extremely rare on these islands. In the spring and fall, however, the great numbers of migrating birds which stop here no doubt devour many of these large Orthoptera in spite of their almost perfect concealment. But for their protective resemblance and habits birds might easily exterminate such slow-moving flightless insects within a few seasons, in fact the existence of creatures like *Aplopi* on these small islands is really dependent upon their ability to be passed unobserved by birds migrating between the eastern United States, West Indies and South America.

The question arises whether the protective behavior in *Aplopus* is fully developed on hatching from the egg or whether it is attained with their large size and mature condition. In order to

[1] "Habits, Reactions and Mating Instincts of the 'Walking-Stick,' *Aplopus mayeri*," *Science*, N. S., XXVII., 1908—Publication No. 103, Carnegie Institution, Washington, 1908.

investigate this and the further question of first-leg form considered below eggs were collected during the summer and brought to New York where the newly hatched individuals might be observed.

These eggs were kept in small loosely stoppered bottles in the laboratory at ordinary room temperature. They began hatching about the first of December and during January a large number of the insects came out.

Behavior of Newly Hatched Aplopi.

The reactions of the small insect on the day it emerges from the egg are almost identical with those of the fully mature eight-inch females which I studied at the Tortugas. The young *Aplopi* are a light chocolate-brown in color with yellowish bands about the legs and the sexes are similar. The adult males, however, become greenish in color while the female retains her original brown. The adults also have rudimentary wings which are capable of being raised when the insect is excited, but the young are wingless. Their reactions will be referred to briefly at this time as they are given in some detail in my former paper.

The insects when at rest among the twigs assume an attitude which in consequence of their stick-like shape makes them most difficult to detect. The first pair of legs are stretched directly forward enclosing the head between thin curved portions of the femora which fit perfectly against it. The antennæ are brought

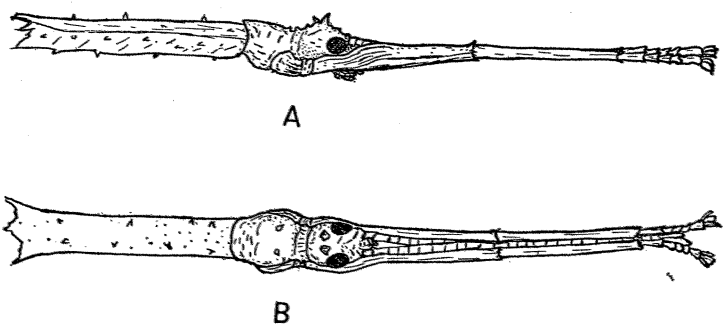

Fig. 1. *A*. Lateral aspect of *Aplopus*, head and first two thoracic segments. The first pair of legs are stretched forward in the typical resting attitude. The femur fits perfectly about the ventro-lateral region of the head and leaves the eyes uncovered.

B. Dorsal view of the same specimen showing the approximated antennæ directed forward and enclosed between the first pair of legs.

together between the first legs, Fig. 1, *B*. (See also Fig. 1, Plate I., and the photographs in my former paper.) The anterior end of the insect thus closely resembles a more or less pointed stick. The newly hatched individual habitually assumes this position and the point of especial interest, which I shall return to later, is that the thinned out curved part of the femora fit about the head as perfectly the first time the legs are stretched forward as they do in the adult.

In walking from place to place the adult moves slowly and often exhibits a slow laterally swinging motion suggesting a twig swinging in a light breeze. The young also swings its body from side to side in a similar manner. When a number of young *Aplopi* are sitting motionless if the observer blows a current of air over them they all begin to swing very actively from side to side as if being swung by the breeze. This swinging motion no doubt serves to render them less conspicuous among the shrubs.

The newly hatched individuals use the same methods to escape an enemy as those employed by the adult. When they are touched or pinched slightly they move away a short distance and immediately come to rest again, if the stimulus be repeated they begin to walk at a more rapid gait than before and move a greater distance away. If again touched they drop bodily to the floor and feign death just as the adult does. The death-feigning reaction is more readily induced in the young than in the adult, and no doubt serves to great advantage in enabling them to escape an enemy which fails to seize them securely in the first attempt. The chances of escape for this stick-like creature when it drops through the dense foliage and branches of the *Suriana* bush is most favorable. When in the death-feint the legs may be bent in any position and the body twisted without the least move on the part of the animal. They may actually be piled one on another and will remain as motionless as dead insects.

The young walking-stick crawls upwards on any object that it may reach after emerging from the egg. As I previously recorded the female *Aplopus* sits in the *Suriana* bushes and lays its eggs which fall to the ground where they later hatch. Thus the tendency of the young to crawl upwards on the first object with which it comes in contact serves to bring it up the *Suriana* bush

to its leafy food. In crawling up the young insect waves its antennæ to feel the way just as does the adult and reaches out with the first legs to grasp the object located by the antennæ.

Finally the young like the adult is more or less nocturnal in its movements. During the day they sit motionless with the first legs extended forward but at night they become active and move about to feed. The food of the adult is limited to the leaves of *Suriana*. I have made no attempt to feed the young since they may be kept alive for about one week after hatching without taking food.

The Thin Curve of the Femora which Fits Against the Ventro-Lateral Surfaces of the Head.

When the first pair of legs are extended forward the femur of each is so curved near its proximal joint as to fit perfectly against the ventro-lateral parts of the head and at the same time leaves the eyes uncovered, Fig. 1, *A* and *B*. The curved portion of the femur is also very thin in a lateral direction and thus when pressed closely to the head the legs go out as almost straight lines instead of bulging around the head to any great extent. It seems difficult to believe that the first pair of legs could through chance variations or mutations have come to fit so perfectly around the sides of the head and at the same time to have their dorsal line so curved as to leave the eyes uncovered. It must be remembered that when the first legs are in the extended position the head presses against the dorso-lateral surfaces of the femur and not straight against the inner lateral surface only. This arrangement may be better understood by a close examination of the dorsal and lateral views given in Fig. 1, *A* and *B*.

The possibility suggests itself that the perfection of the fit is attained during the life of the individual since the legs are so habitually pressed against the head for about twelve hours daily. To test this it became desirable to study newly hatched individuals in order to find whether the femur curve was as perfectly adjusted in them as in the adult. A careful examination of about one hundred *Aplopi* shortly after emerging from the egg has convinced me that the curve of the femur is as true to the head pattern in the newly hatched young as in the mature insect when several months old.

Finally, is this adjustment between the structure of the femora and head due to the position of the insect when enclosed within the inelastic egg shell? If the first legs were folded forward against the head the pressure during embryonic life might easily be sufficient to mold the femur curve into pattern for the head. Twenty eggs containing embryos at various stages shortly preceding hatching were dissected with this question in view. The elliptical egg shell is of a rigid chitinous material with a circular operculum at one end and a hilum-like scar on one side to which the

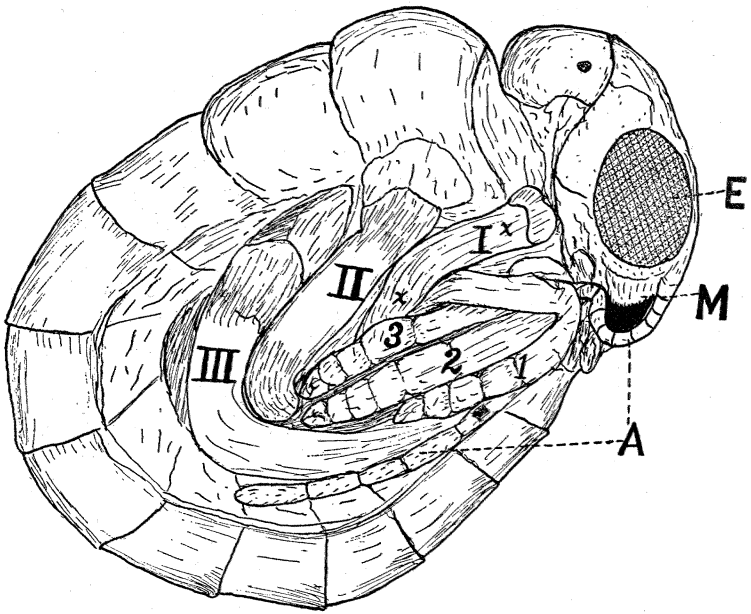

FIG. 2. An unhatched *Aplopus* with its egg membranes dissected away showing its folded position. The femora of the three right legs are marked with roman numerals and the tarsal ends of the same legs are indicated by figures. The part of the first femur which in later life fits against the head is shown between the points *x–x*, it is not molded against the head in the egg. *A*, antennæ; *E*, compound eye; *M*, mandible.

inner egg membrane is attached. The size of the egg ranges from 2 mm. in narrow diameter by 4 mm. in long diameter to 3 mm. by 4.5 mm. The length of the walking-stick on hatching is from 17 mm. to 23 mm. measured from the tip of abdomen to tip of the first pair of legs when extended forward, or from tip of head to tip of tail 9.5 mm. to 13 mm. The embryo within the egg is, therefore, necessarily much folded and bent.

On dissecting the egg the embryo is found to be curled around in a rather constant manner, the head being usually, though not always, near the opercular end. The long legs are folded back and forth upon themselves in a very definite fashion as shown by the camera drawing, Fig. 2. The antennæ (*A*) pass down the front of the head and then back along the ventro-lateral surface of the abdomen being sometimes bent around the first pair of legs. The point of most importance is that the femoral segments of the legs are all directed obliquely away from the head. The first pair of legs each of which is folded on itself four times does not touch the sides of the head at all. The head and large eyes are entirely uncovered and exposed. The femora of the first pair of legs not only fail to mold their curves against the head but the femora are so pressed against the thorax that the surfaces which will subsequently be concave (in Fig. 2 between *x* and *x*) are actually arched convexly. Thus it is seen that the mechanical arrangement of the embryo's parts within the egg is not responsible for the fit of the femur curve against the head. On the contrary the curve seems to develop in spite of these arrangements.

When hatching the embryo's head and body come forth from the egg first, the antennæ are then pulled out, the legs being the last parts liberated from the shell, Fig. 3. It often happens that the shell is carried around for some time dangling to the third pair of legs. In Fig. 3 the well developed curves of the femora are distinctly shown, *x* to *x*, and are being pulled in a direction away from the head, yet as soon as the legs are free from the shell the first pair may be straightened forward and their curved femora fit neatly against the sides of the head. We see, therefore, that the curve of the femora to fit the sides of the head is a character transmitted to all of the young and perfectly formed at the time of hatching. It might seem that the origin of this character was most probably due to the habit of the insects to press the first pair of legs against the head. Gradually this pressure developed a thin concave region of the femur of the first leg which molded itself more and more perfectly to the contour of the head. If this curve arose in any other way the second and third pairs of legs might have developed at least a trace of such a character though this is not absolutely necessary. It must be

remembered that the curves fit the ventro-lateral contour of the head to a remarkable degree.

When the first pair of legs are so stretched forward the insect's antennæ are brought together. The legs have an irregular groove extending along the approximated surfaces and when complete approximation takes place a rather imperfect tube is formed enclosing the antennæ. This is a case analogous to the above and it is difficult to imagine how chance variations could

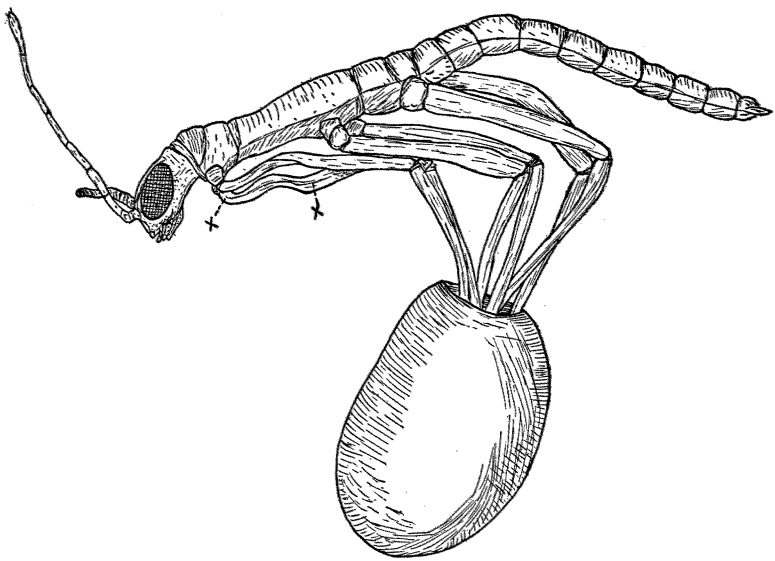

FIG. 3. *Aplopus* in the act of hatching from the egg. The body and head come out first, then the antennæ and finally the legs free themselves from the shell. The parts of the first legs between *x*–*x* are curved to fit the head when they are straightened forward although they have never touched the head up to this time.

bring about such mechanical harmonies between organs only associated through an habitual attitude assumed by the animal when at rest. Yet it must not be forgotten that many other equally as nice morphological arrangements exist which have no habit or action connected with them. Indeed a crucial case of use inheritance is almost impossible to imagine from purely descriptive work. I would not be understood as advocating any principle of inheritance but merely bring forward the present case as being of interest in itself.

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